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Surviving drought: a framework for understanding animal responses to small rain events in the arid zone

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Surviving drought: a framework for understanding animal responses to small rain events in the arid zone

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Key words: arthropod; buffer; desert; herbivore; pulse-reserve; soil.

INTRODUCTION

Arid zones are characterized by stressful climate conditions, including large seasonal variation in temperatures, and highly unpredictable fluctuations in rain epitomized by the simple pulse-reserve model of ecosystem change developed for large changes in rainfall (Noy-Meir 1973). Rain events influence nutrient cycling and the structure of arid-zone animal and plant communities in a complex fashion, dependent on the timing, magnitude, and duration of rainfall, as well as local abiotic (soil type) and biotic (community type) conditions (Reynolds et al. 2004, Morton et al. 2011, Nano and Pavey 2013, Jentsch and White 2019). Long-term abundance

data from populations of butterflies, small mammals, and arthropod pests suggest that the simple accumulation of large annual increases in rain can result in dramatic increases in some animal populations, particularly in invasive species, or animals with high rates of reproduction (Ouyang et al. 2014, Harrison et al. 2015, Veran et al. 2015, Greenville et al. 2016). However, weather data often poorly predict fluctuations in the abundance of many higher taxa (Knape and de Valpine 2010, Herando-Pérez et al. 2014). Often, arid-zone rain events are not considered biologically significant without subsequent increases in plant growth (Reynolds et al. 2004). Nevertheless, there is some evidence that short-term pulses of rain may be a process that can buffer populations from decline or local extinction during drought (Maron et al. 2015). For species able to take advantage of small rain events, population abundances can be maintained at higher levels through time than if a pulse of rain had not occurred, providing longer-term benefits

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to these buffered populations. In drought-prone northern China, short-term increases in temperature and irrigation produced a cotton bollworm (*Helicoverpa armigera*) outbreak in 1992, which resulted in the establishment of a higher equilibrium population size for the species and more frequent outbreaks of the pest (Ouyang et al. 2014). Thus, the importance of small rain events over longer-term drought may be critical in maintaining arid-zone populations.

We propose a conceptual model of responses of organisms to small-scale rain events that conceptualizes the ideas that some organisms will be buffered from an overall drought and that small-scale rain events are very important for the ability of ecosystems to survive drought and recover quickly after drought (Fig. 1). The aim of this model is to help identify the functional guilds of animals that are likely to be unresponsive, responsive in the short-term, and well buffered from the effects of longer-term drought. Our model provides a framework in which to consider the ecological and life-history characteristics that are important in coping with drought.

The longer-term advantage of a pulse of rain is likely to vary across animals in response to differences in life history and ecology. For example, species with lower

fecundity, longer generations, or longer-lived species may have high population densities following rain for longer periods of time than species with shorter generations that track resources more closely (Schwinning and Sala 2004, Morris et al. 2008). Alternatively, rapid responses to rain fluctuations can be disadvantageous when the animal population fails to complete a full generation before resources decline, resulting in a “developmental trap” (Van Dyck et al. 2015). Desert plants have dormancy periods to avoid germination following insufficient rain that could result in high seedling mortality (Rathcke and Lacey 1985). Similar selection pressures may explain why some species, particularly insect herbivores, have evolved a delayed response or are unresponsive to small rain cues but retain a strong response to temperature cues that control preferred food plant growth (Bale et al. 2002, Harrison et al. 2015). Smaller rain events result in increased microbe and fungal productivity, but may be less likely to result in significant plant productivity important to herbivores and their predators (Reynolds et al. 2004, Schwinning and Sala 2004, Collins et al. 2014). Therefore, small rain events may provide resources that benefit some animals, but many may differ in their timing and magnitude of

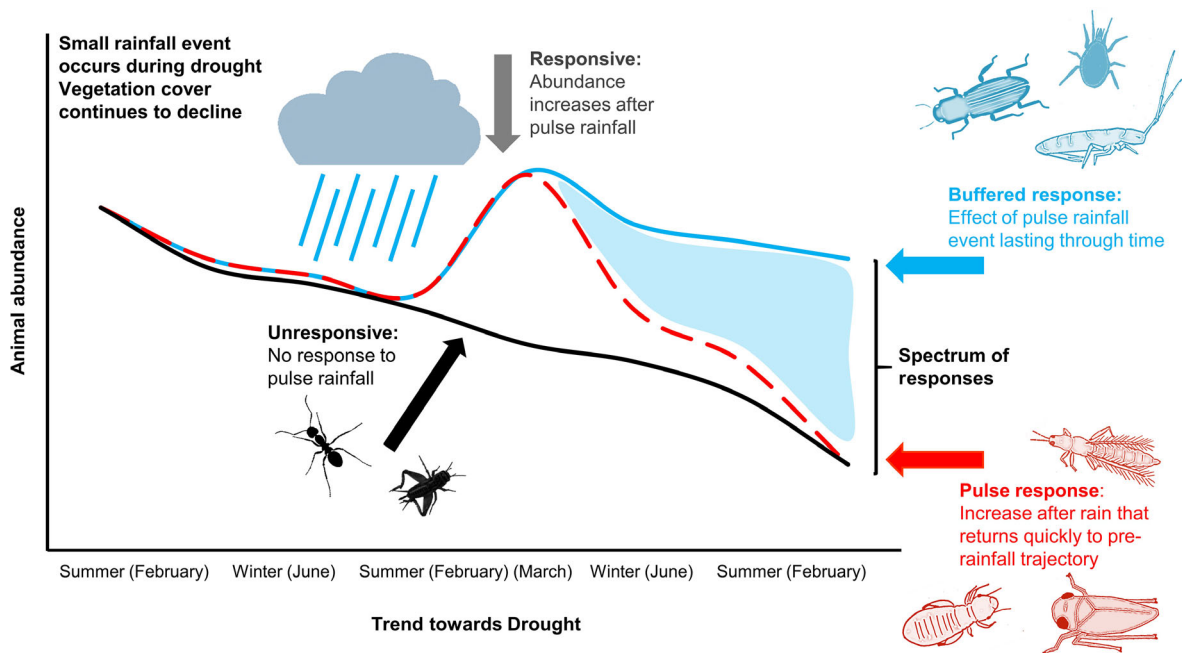


FIG. 1. A simplified model of animal responses to small rain events that interrupt long-term drought, but do not halt declines in primary productivity. Arthropod populations may be unresponsive to rain, not respond, and continue to decline (or show an increase not shown here) (Unresponsive: black line). Other populations may be responsive and increase in abundance following rain (Responsive), but vary in their subsequent response, with a spectrum spanning those that rapidly decline (Pulse response: dashed red line) following the initial pulse response, and those that maintain a high abundance post-rain (Buffered response: solid blue line), apparently buffered against large declines over a longer period. To measure the response type of different arthropod taxa, this study used pitfall sampling during a high-rainfall year (summer and winter) before the pulse rain event, immediately before and after the summer rain event, 3 months after the event during low rainfall winter, and a year after the rain event in summer. Representative arthropod groups are illustrated for each type or spectrum of responses.

responses. It is likely that animal populations living under drought conditions will respond to small rain events in fundamentally different ways. There are two likely primary responses of animals to small rain events (Fig. 1):

- 1) Animals that are *Unresponsive* to rain and maintain a population abundance trajectory (i.e., populations remain stable, fluctuate in response to other variables or continue to decline during drought, showing no shift from pre-rain trajectories).
- 2) Animals that are *Responsive* to rain and show a shift from the pre-rain trajectory, with the post-rain timing, magnitude, and duration of population abundance trajectory variable depending on taxa life history, density effects, or species interactions.

An investigation into the effects of pesticides applied for locust control on the arthropod fauna of an arid landscape in western NSW Australia provided the opportunity to utilize the control (unsprayed) site data to investigate the population-level responses of ground-dwelling arthropods to rain (Maute et al. 2017a). Using data from this replicated field experiment, the current study tested the comparative effects of interannual and short-term rain and season on terrestrial arthropods in the arid zone of Australia. We assessed the impact of the onset of drought conditions over 2 yr by using pitfall trap captures to monitor populations during summer and winter. Captures were recorded before and after a significant short-term rain event that interrupted drought conditions in the second summer of the study.

METHODS

The study was conducted at Fowlers Gap Arid Zone Research Station (31.087034° S, 141.792201° E) NSW Australia. The property is a working sheep station managed for biodiversity conservation and research, including the nontarget impacts of locust control pesticides on a range of fauna and ecosystem services (Maute et al. 2015, 2016, 2017b). All sites selected were located in arid grassland habitat dominated by perennial native grasses (such as *Astrebula* spp. and *Dichanthium* spp.) and low shrubs (Chenopodiaceae), and were grazed by sheep and native kangaroo species. The site has cool winters and hot summers (average maximum and minimum temperatures: winter, 4–17°C; summer, 19–34°C). Mean annual rainfall was 250 mm and rainfall during the study was 526.2 mm in 2011, 322 mm in 2012, and 98 mm in 2013; a trend from above-average rainfall towards drought (Australian Bureau of Meteorology).

To monitor the effects of time and rain on arid-zone arthropods, we used a random block experimental design. Three 1-km-diameter circular sites (79 ha) were at least 4.5 km apart to ensure independence of sampling. Within each site we established six arrays in a pattern including a center array and five perimeter arrays,

all >200 m apart and placed randomly. This resulted in $n = 18$ replicate arrays. Each array consisted of 12 pitfall traps (67 × 84 mm plastic containers filled with 100 mL propylene glycol) in a cross formation at 8, 24, and 40 m from a central stake (Appendix S1: Fig. S1). Each trap was open for 72 h. Sites were sampled on a staggered schedule within each of four sessions, over a period of up to 20 d. Sessions occurred in February 2012, late June 2012, February 2013, March 2013, late June 2013, and February 2014. After 72 h, pitfall containers were sealed and stored. All insects were identified to subclass or order, and abundant taxa were subdivided further. Hymenopterans were divided into formicids and non-formicids (formicids were identified to genus or species). Formicidae species results are presented as a supplement. Collembolans were divided into the three orders (Poduromorpha, Entomobryomorpha, and Symphypleona). Orthopterans were divided into acridids and gryllids.

Mean temperature (month) and rain (Appendix S1: Fig. S2) were recorded during the study period. A small rain event (20–40 mm) occurred over 10 d in late February 2013 (Appendix S1: Fig. S2), and all sites were sampled directly before and within 3 weeks afterwards. We report a range of rain depth values based on the minimum rain recorded, and a likely maximum, as rain was heterogeneous across sites. Although our aim was not to define large vs. small rain events, the 20–40-mm rain event was small compared to the larger and more continuous rain events of 2011–2012 that totaled more than 500 mm, and was in contrast to the <100 mm rain between 2013–2014 (Appendix S1: Fig. S3). The 20–40-mm event in 2013 was within the 75–90% quartile of rain events at this site, but was not observed to result in significant plant growth, in contrast to larger rain events which occurred in 2011–2012.

Statistical Analysis For each arthropod taxon, capture data for each trapping session were pooled for the 12 pitfall traps in each array and $\log(x + 1)$ transformed to account for positive skew. Using Spearman's correlations, we found that yearly rain measures were negatively correlated with temperature (yearly rain Spearman's $\rho = -0.49$, $P = <0.0001$), as more rain occurred in winter in 2012, 2013, but not 2011. Because of the lack of independence between temperature and rain, and the low number of trapping sessions ($n = 6$), we did not test the effect of climate on arthropod populations using correlations between arthropod abundance and raw temperature or rain values. Instead, each trapping session was identified as either summer or winter, and as a high or low rain year. These broad categories were then used in subsequent analysis of the effects of weather on arthropods using JMP Pro11.0.0 (SAS Institute).

We investigated the short-term (<3 week) effect of a significant rain event (20–40 mm) which occurred in late February 2013 (Before = Feb2013, After = March2013). Changes in abundance of the 15 most abundant arthropod taxa in response to the short-term rain event were

tested using repeated-measures restricted maximum likelihood (REML) random effect models with time (before or after) as a fixed effect, and array nested in site as a random effect. The direction of significant differences among sessions was determined by post hoc Tukey honestly significant difference.

We also explored both the longer-term (2-yr) effects of season (summer trapping in February 2012, 2014 vs. winter trapping in June 2012, 2013) and yearly rain (high rain in 2012 vs. low rain in 2013, 2014) on arthropod abundance. The longer-term effects of climate on arthropod and ant taxa were tested using $\log(x + 1)$ transformed abundance data in repeated-measures REML models with season (summer, winter) and annual rainfall (high, low) as fixed effects, and array nested in site as a random effect.

When significant effects of rain were detected, the direction and magnitude of temporal changes in abundance of individual taxa were calculated as percent change, based on differences between raw capture abundance data between the immediate pre-rain sampling period and the three post-rain sampling periods. These figures are provided as an explanatory tool for significant results based on models described above, to clarify how similar arthropod numbers were before and after the rain event and whether the rate of decline was similar in the year proceeding the rain event compared to the year following. Post hoc tests of differences among trapping sessions suggested if measures returned to lower pre-rain levels.

RESULTS

Approximately 736,217 arthropods from 26 orders were collected over 2 yr. Most arthropod captures were from three taxa: collembola, formicid hymenoptera (ants), and acari (mites), with each of another 10 abundant arthropod taxa contributing <3.1% of captures (Appendix S1; Table S1). The small rain event produced a positive response of 10 taxa within 2 weeks post-rain, suggesting that these taxa benefited in the short term (Table 1). In contrast, there was a negative response for Blattodea (roaches), and no response for ants, Diptera (flies), hemipterans, and crickets (Grillidae; Table 1), all unresponsive to rain. The increase in capture numbers was at least 81% for responsive taxa, but most were orders of magnitude higher (Table 1). Entomobryomorpha and Symphyleona Collembola, Coleoptera (beetles), Araneae (spider), and mite abundance remained elevated (and possibly buffered from declines) in winter, 3 months post-rain (Table 1, Fig. 2). However, only beetle and mite abundance remained significantly elevated (buffered) 12 months later in 2014 (Table 1, Fig. 2). Most beetles captured after the rain event were small (<1 mm) Tenebrionidae (KM, *personal observation*). Despite the high magnitude of increases directly after rain, Poduromorpha Collembola, nonformicid Hymenoptera (wasps), homopteran, psocopteran, and thysanopteran

abundance returned to levels similar to winter 2012 (high rainfall) or lower within 3 months (winter low; Fig. 2). These taxa continued to decline in 2014 or were stable (Table 1, Fig. 2), representing a short-term pulsed response.

Longer-term results show that most taxa displayed an interactive response to season and rain, but Thysanoptera abundance was not significantly related to any factor and Psocoptera and wasp abundance was influenced by each factor independently (Table 1). Poduromorpha and Entomobryomorpha had decreased abundances in response to lower annual rainfall, mainly between the two summer trapping sessions (Table 1, Fig. 2). Ants, crickets and spiders declined during winter and abundance did not increase during summer during low rainfall (Fig. 2). Mites, flies, wasps, Homoptera, and Psocoptera had higher captures in summer seasons, but only during high rainfall for mites and flies and mainly during low rainfall for wasps and homopterans (Fig. 2). During high rainfall, Symphyleona abundance was higher in summer with the opposite being true in low rainfall years (Fig. 2). Hemipteran numbers were higher in winter during high rainfall, but this reversed during low rainfall, whereas roach numbers were only high during the low-rainfall summer (Fig. 2).

DISCUSSION

The abundance of most arthropod taxa displayed one of two immediate responses to short-term rain. Arthropods either dramatically increased in abundance, or showed no response to rain and continued the pre-rain trajectory in abundance, most typically a continued decline (Fig. 1, Responsive or Unresponsive). The majority of taxa declined in abundance over 2 yr, suggesting a long-term negative response to the onset of drought conditions. In the short term, 10 of the 15 most common ordinal taxa increased after the small rain event, with varied benefits, creating a spectrum of responses over the following year (Fig. 1). For some taxa, rain-buffered populations from longer-term population declines, and other taxa only benefited for a short time, suggesting a brief pulsed response to the small rain event (Fig. 1). Although the short temporal scale of our monitoring precludes the use of statistical models investigating changes in abundance in response to longer-term variable weather (Ferguson et al. 2017), the power to detect responses would be higher if both weather and animal abundance were tracked on a finer temporal scale and for longer than 2 yr. However, by identifying which taxa benefited from a small rain event, and for how long, we increased our ability to predict the vulnerability of species to increases in rain variability in the future.

We suggest that the difference in the longevity of arthropod responses to rain was most likely because of the differential influence of season and rain changes on animals with different life histories. For example, the abundance of Entomobryomorpha and Symphyleona

TABLE 1. Probability values for changes in $\log(x + 1)$ arthropod captures in the short term, before and after a small summer rain event (<3 weeks before, after), and over 2 yr, using long-term factors of season (summer, winter), rain (high, low) or season \times rain interaction term.

Arthropod taxa	Short-term effect ($n = 18$, $df = 1,17$) rain P value	% change after small rain event	% change 3 months post-rain	Long-term effect ($n = 18$, $df = 1,51$)			% change 12 months post-rain
				Season \times rain P value	Season P value	Rain P value	
Collembola, Symphypleona (B)	<0.0001*	+12,998%	−88%	<0.0001*	0.05	0.50	48%
C. Poduromorpha (P)	<0.0001*	+10,411,733%	−99%	0.004*	<0.0001*	<0.0001*	−200%
C. Entomobryomorpha (B)	0.0002*	+652%	+73%	<0.0001*	0.09	<0.0001*	−137%
Coleoptera (B)	<0.0001*	+2,993%	−46%	<0.0001*	<0.0001*	<0.0001*	50%
Acari (B)	<0.0001*	+1,409%	−79%	0.004*	<0.0001*	<0.0001*	76%
Araneae (P)	<0.0001*	+81%	−51%	<0.0001*	<0.0001*	0.31	−2%
Psocoptera (P)	0.0007*	+365%	−10%	0.05	<0.0001*	0.002*	93%
Thysanoptera (P)	0.0002*	+2,600%	−11%	0.24	0.45	0.62	95%
Formicidae (U)	0.96			<0.0001*	<0.0001*	<0.0001*	−81%
Nonformicid Hymenoptera (P)	<0.0001*	+103%	−90%	0.18	0.0001*	<0.0001*	−173%
Homoptera (P)	<0.0001*	+420%	−67%	0.02*	0.003*	<0.0001*	6%
Hemiptera (U)	0.07			0.0001*	0.90	<0.0001*	−30%
Gryllidae (U)	0.20			<0.0001*	<0.0001*	<0.0001*	−750%
Diptera (U)	0.36			0.004*	<0.0001*	0.01*	18%
Blattodea (U)	<0.0001*	−94%	−79%	<0.0001*	<0.0001*	<0.0001*	−149%

Notes: Percent changes in raw abundance values were relative to pre-rain levels. Classification of patterns of response to rain; taxa were unresponsive (U), responded within the spectrum of a short-pulsed response (P), or buffered from large decline (B). Significant P values are designated by asterisks.

Collembola, beetles (mainly Tenebrionidae), spiders, and mites increased dramatically after rain (by 1,400 to 13,000%). After 3 or even 12 months, the abundance of these five taxa declined slightly, but remained higher than pre-rain, despite the change to winter season conditions and continued drought. These taxa included mainly small soil-dwelling organisms that would benefit greatly from increases in soil microbial activity, which occurs after as little as 2 mm of rain (Whitford et al. 1981, Schwinning and Sala 2004, Henschel et al. 2007, Wu et al. 2014). A diet of bacteria, fungi, and/or microorganisms may explain the longer persistence of these taxa in an arid environment than larger or specialized arthropods that live above the soil surface or are dependent on plant productivity.

In contrast, Poduromorpha collembolan, hymenopteran (wasp), homopteran, psocopteran, and thysanopteran abundance also increased dramatically after rain (by 80–10.4 million%), but quickly returned to low abundance after 3 months. Collembolans, homopterans, psocopterans, and thysanopterans are more likely to be reliant on plants for both food and shelter, and only slight increases in plant productivity were observed at our sites. In addition, the increase in predatory spiders, mites, and wasps may have produced substantial, top-down suppression on prey species, similar to interactions among mammalian predators and prey (Holmgren et al. 2006, Greenville et al. 2017). These differences in life

history may explain the shorter pulsed response of some taxa to a small rain event. However, all responding arthropods must share the trait of rapid reproductive cycles in order for these dramatic changes in population sizes to occur over such a short time frame. These findings not only highlight the differences in the abilities of arid-zone fauna to capitalize on resources provided by small rain events, but also the likelihood that increases in other arid animal populations could be missed using infrequent sampling.

A recent analysis of temporal changes in arthropod populations in a sandy desert in Australia found that ants, Collembola, and mites responded to long-term rain and vegetation productivity and not short-term rain, despite a frequent sampling protocol (Kwok et al. 2016). However, the findings of the current study suggest a pattern of rapid increase and decline is possible on a short time scale for Australian arid-zone arthropods. In contrast to Kwok et al. (2016), our study was conducted in arid shrubland dominated by fine-textured soil, which can hold moisture longer than coarse sandy soil and is more able to retain basic nutrients such as carbon, nitrogen, and phosphorous, which are important to microbe and plant growth (Austin et al. 2004, Nano and Pavey 2013). The higher water-holding capacity and nutrient levels that characterize fine-textured soils would have created a larger increase in primary resources available to arthropods during small rain events. We suggest that

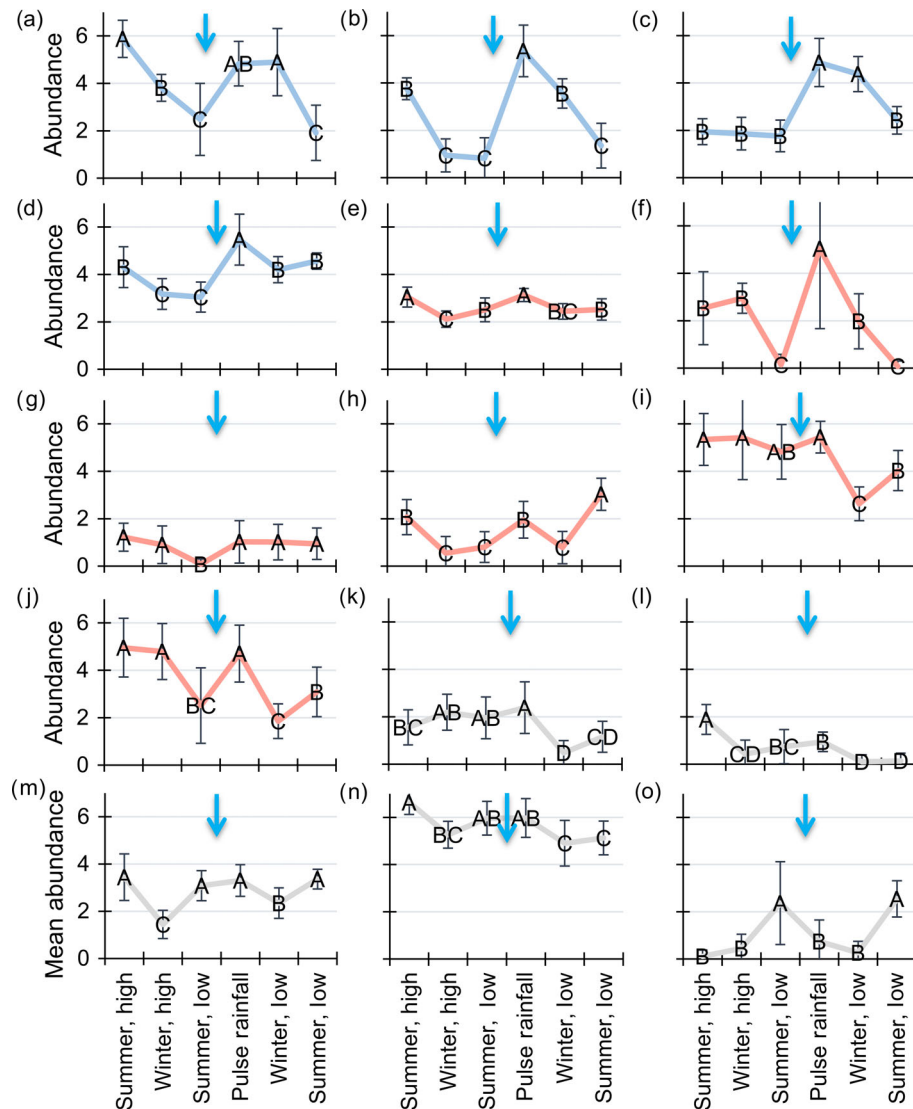


FIG. 2. Abundance of 15 key arthropod taxa over six trapping sessions. Points represent mean abundance measures ($\log(x + 1)$ transformed \pm SD) for all trapping sessions, which are identified by season and yearly rain classification. Letters show significant differences among abundance during different trapping sessions, based on Tukey-Kramer honestly significant difference. Downward-facing arrows indicate when the pulse summer rain event took place. Graphs refer to abundance values for (a) Collembola, Entomobryomorpha; (b) Collembola Symphypleona; (c) Coleoptera; (d) Acari; (e) Araneae; (f) Collembola, Poduromorpha; (g) Thysanoptera; (h) Psocoptera; (i) nonformicid Hymenoptera; (j) Homoptera; (k) Hemiptera (l) Gryllidae; (m) Diptera; (n) Formicidae; and (o) Blattodea. Taxa that were unresponsive have gray trend lines, pulsed responses are shaded pink, and buffered taxa are shaded blue.

the rapid increases in arthropod abundance we observed were driven by a rain event that was of an insufficient magnitude to elicit significant perennial plant responses, but caused a sufficient increase in the activity of soil microbes and annual plants to provide temporary resources for breeding invertebrates (Schwinning and Sala 2004).

The trend toward a buffering effect of the small rainfall event that resulted in reduced population declines for several taxa suggests that these organisms may possess traits that allow them to benefit from resource

pulses for longer periods. Based on studies of plant and vertebrate traits, it is likely that the soil arthropod taxa we found to benefit most from a small amount of rain were relatively longer lived, unsuppressed by predators, and/or had a more generalist diet (Chesson et al. 2004, Morris et al. 2008, Angert et al. 2011, Slatyer et al. 2013). More detailed life-history information on the particular species inhabiting the site would be necessary to test this hypothesis and better identify the traits linked to positive responses to small rain events. The identity of beneficial traits could then be used to assist predictions

concerning the vulnerability of species to increases in rain variability, an impact of climate change.

Five ordinal taxa did not show a positive response to the small rain event, all of which were plant-feeding insects or ants. Previous research has shown that some arid-zone animals show a time lag in increases after rain due to delayed perennial plant productivity on which they heavily rely for survival and reproduction (Ayal 1994, Greenville et al. 2013, Kwok et al. 2016). If the small rain event documented in our study was not sufficient to cause an increase in plant productivity, this may explain the lack of a positive response from larger herbivorous insects such as crickets and hemipterans, which only displayed responses to longer-term changes in rain. These arthropods may also reproduce more slowly, suggesting that their life-history traits did not allow these taxa to take advantage of short, small rain events of 20–40 mm, similar to higher vertebrate herbivores (Greenville et al. 2013). Indeed, Walker et al. (2016) did not find a significant increase in Formicidae abundance after significant rain in similar arid grasslands of Australia.

Overall, the differential responses of arthropod taxa to both longer-term drought and small, short rain events suggest that some taxa are more at risk of decline and extirpation during drought than others. Plant-dependent herbivores such as crickets showed little evidence of positive responses to a small rain event, suggesting they are vulnerable to decline during longer-term droughts. However, our sampling regime inadvertently favors detection of pulse increases and declines in the fastest-responding taxa. It is possible that our sampling failed to detect increases in taxa that had a delayed increase after rain, but then rapidly declined. The generation time for some cricket species can be as short as 2 months from egg laying to breeding of new adults (Zajitschek et al. 2009), and a breeding event could have occurred within the 3-month gap in our sampling periods (Fig. 1). However, we propose that it is unlikely that the resulting adult populations would then crash and be undetectable within 3 weeks after reaching maturity, as adults typically live 4–6 weeks (Zajitschek et al. 2009). In addition, perennial plants were not observed to invest in substantial new growth after the small rain event. During the 2 yr of this study, we observed a decrease in grass and shrub cover, and a lack of flowering and seeding in many perennial species in the second year. The finding that herbivore declines were pronounced during a period of drought and lower plant productivity agrees with reviews of the fundamental causes of fauna extinction being linked more closely to changes in food availability, not directly with changes in rain (Cahill et al. 2012).

Not all taxa showed a decline during drought. The negative response of roaches to both short- and longer-term rain was unique and intense. Roach captures were low during the high-rain year and winter, but increased by 548% during the hottest and driest summer trapping session in 2014. Roach activity may have simply increased due to a preference for warm weather or a

reduction in plant cover after drought. Though psocopteran abundance also increased at this time, these taxa were common in both high and low rain years, and responded positively to short-term rain, suggesting that summer increases were driven by a seasonal change in abundance, possibly because of simple changes in temperature. It is also possible that increases in roach captures may represent a behavioral response to our traps, not an abundance-driven response to environmental conditions. Desert roaches are nocturnal and prone to desiccation unless they can shelter in microclimates that allow the absorption of water vapor at high humidity (Hawke and Farley 1973). During extreme heat and drought, these microclimates may be more difficult to locate, and roaches may also seek water. If true, it is possible that the propylene glycol in our traps acted as an attractant.

The seasonal timing of decline during drought also differed over the long term among taxa and could be related to life-history traits such as diet and seasonal activity patterns. Homopteran and hemipteran abundance remained high during the higher rain year, but dropped significantly in the low rain year (particularly in winter) when primary productivity important to these herbivores may have been at its lowest level. In contrast, ant, spider, and cricket numbers declined sharply during the first winter and remained at similarly lower abundance during the subsequent low-rain summer and winter, suggesting that reduced temperature or solar radiation may have been an important influence on abundance (Bowden et al. 2018). Mites, flies, and psocopterans declined during winter, but increased in summer, suggesting that their abundance was less influenced by rainfall than seasonal temperature fluctuations.

CONCLUSIONS

Our findings provide the framework for a new model of invertebrate responses to environmental conditions in the arid zone. Previous pulse-reserve models of the influence of weather and abiotic conditions on arid-zone plants and animals mainly focus on significant triggers of pulse events and acknowledge that multiple factors will feed back into the patterns of animal population responses (Noy-Meir 1973, Reynolds et al. 2004, Peters and Havstad 2006, Nano and Pavey 2013). Although general pulse dynamic theory describes all magnitudes of events (Jentsch and White 2019), most arid-zone studies do not clearly outline the likely patterns of animal population responses in the aftermath of resource pulses (but see soil microbe and small mammal population dynamics (Schwinning and Sala 2004, Holmgren et al. 2006, Collins et al. 2014). We show that not only do most arid-zone arthropod taxa respond to longer-term patterns in rain as predicted by simple pulse-reserve models, but a short-term “pulsed or buffered” pattern of rapid population increase followed by fast or slow decline is possible in response to small rain events that

do not result in increased primary productivity in plants. In addition, the lack of consistent arthropod responses to climate over 2 yr suggest the need for more detailed long-term monitoring and analysis of the environmental conditions which support both sensitive and resilient arthropod taxa. Such monitoring efforts would enable the robust testing of our model in the future.

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Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2884/supinfo>

DATA AVAILABILITY

Data are available on the Dryad Digital Repository: <https://doi.org/10.5061/dryad.2k54f0d>